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Host-parasite nestedness a result of co-evolving trait-values

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Abstract

Nestedness is an intriguing feature of ecological networks, where those species found in species-depauperate communities are subsets of those found in communities with greater species richness. For bipartite interaction networks, a “community” of species may be thought of as all those pollinating a particular plant, or infecting a particular host, for example. While there is much clear evidence for nestedness in mutualistic webs, host-parasite webs have proven more contentious. There have been a number of suggested causes for nestedness, including an association between the abundance of individuals and the resulting number of species interactions, and the matching of phenotypic traits between species. Questions remain as to the relative importance of these driving factors, especially as host-parasite and mutualistic webs contain completely different interaction types.

We propose a model motivated by both of the above factors, considering a trade-off in resources that a species faces in optimizing its transmission or defense. We construct a multi-species model in which both hosts and parasites have limited resources with which to attack or defend themselves from each other. We analyze the evolution of the manner in which they use these resources using adaptive dynamics, to arrive at a final species interaction matrix, which we then test for nestedness. A general model with m hosts and n microparasite species is described here, but results are given for $m = n = 5$, chosen to be a large enough system for patterns to be identified, but not so large that computational time becomes prohibitive.

Our results demonstrate that this co-evolution leads to an unusual amount of nestedness when the trade-offs in transmission for parasites are concave, and an unusual amount of anti-nestedness when they are convex. This enables us to predict the circumstances under which we would expect to observe nestedness in real networks.

Keywords: co-evolution, host-parasite, nestedness, trade-off

1. Introduction

Perfect nestedness in a host-parasite interaction matrix is defined as the case where the parasite species compositions in hosts containing few species are subsets of the parasite species compositions in hosts containing many species (Patterson and Atmar, 1986; Ulrich et al., 2009). A similar pattern, called specialization asymmetry, is present if specialist hosts interact with generalist parasites, and specialist parasites interact with generalist hosts (Corso et al., 2008).

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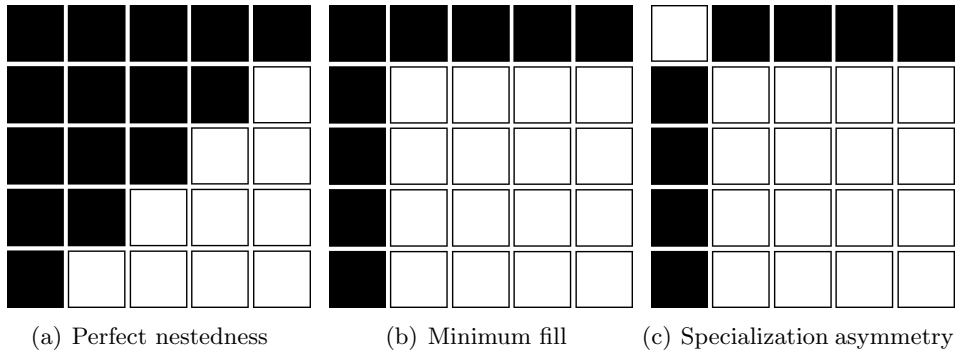


Figure 1: Examples of nestedness and specialization asymmetry. In this case, columns represent one type of species (for example, host species) while rows represent another (for example, parasite species). A filled square represents interactions between the appropriate species, and an empty square indicates that no interactions occur. The first two of these examples display both properties, where (a) demonstrates perfect nestedness and specialization asymmetry, while (b) demonstrates the same at minimum fill. The final example (c) shows specialization asymmetry but not nestedness (according to whether or not the definition of nestedness requires species-poor assemblages to be subsets or proper subsets of species-rich assemblages).

This will lead to nestedness if generalist parasites and hosts also interact with one another (see Fig. 1). There has been evidence for both patterns in host-parasite networks (Poulin, 1997; Vázquez et al., 2005).

Nestedness has come to be regarded as an increasingly important concept in the study of ecological systems, and is one of the most studied aspects of bipartite networks (Corso et al., 2008), yet it is fraught with controversy (Almeida-Neto and Ulrich, 2011; Corso et al., 2008; Greve and Chown, 2006; Podani and Schmera, 2012; Rodríguez-Gironés and Santamaría, 2006). It is, verbally, a well-defined and understood concept, as demonstrated above. Mathematically, however, it has proved difficult to measure (see Almeida-Neto et al. 2008; Almeida-Neto and Ulrich 2011; Araujo et al. 2010a; Atmar and Patterson 1993; Brualdi and Sanderson 1999; Corso et al. 2008; Cutler 1991; Galeano et al. 2009; Podani and Schmera 2011; Wright and Reeves 1992). A large number of different metrics have been devised that aim to measure nestedness, and there is no over-riding best-choice (Almeida-Neto et al., 2008). Metrics measure nestedness in a number of ways, counting unexpected species presences, or species absences, or the number of supersets, amongst others (Ulrich et al., 2009). Hence a variety of metrics is used here, each of which measures nestedness, and therefore anti-nestedness (see section 5), in a different manner. A thorough review of the topic is available in Ulrich et al. (2009), with additional comments in Ulrich and Gotelli (2007) and Podani and Schmera (2012).

A variety of studies across a range of interaction and habitat types claim to have found nestedness (Bascompte et al. 2003; Duponte et al. 2003; Guimarães Jr et al. 2006, 2007; Ollerton et al. 2003; Poulin 1997; Santamaría and Rodríguez-Gironés 2007; Vázquez et al. 2005, although see Dormann et al. 2009; Ulrich and Gotelli 2007; Worthen and Rohde 1996), from scavenger communities (Selva and Fortuna, 2007) to anemonefish and anemones (Ollerton et al., 2007). The majority of these use either the temperature metric of Atmar and Patterson (1993), or a metric based on its basic principle. However, more recently both Graham et al. (2009) and Joppa et al. (2010) have found patterns of nestedness in a range of mutualistic, host-parasitoid and host-parasite networks using the NODF metric (Almeida-Neto et al., 2008). These studies were

the largest we know of to date performed on interaction matrices, and were careful to bear in mind the caveats of previous works.

The work of Joppa et al. (2010) in particular used both the temperature and NODF metrics, as well as a number of null models for comparison. Using the most appropriate null model, the temperature metric discovered more nested networks than expected by chance alone, while NODF found more nested mutualistic networks and both more nested and anti-nested host-parasitoid networks than expected by chance (Joppa et al., 2010). These results agree with Bascompte and Jordano (2007), stating that, although the addition of parasites should increase nestedness (Lafferty et al., 2006), we would expect mutualistic networks to be significantly more nested than antagonistic networks, which are often compartmentalized (Lewinsohn et al., 2006). Hence, we hope to find in our model both significantly more significantly nested and significantly more significantly anti-nested host-parasite networks than expected by chance.

There is much debate on the causes of nestedness in interaction networks, with suggestions of species abundance, phenotypic complementarity and asymmetric interaction strength as the primary potential driving forces (Almeida-Neto and Ulrich, 2011; Bascompte and Jordano, 2007; Ulrich et al., 2009). These can be explained as follows. Firstly, it is assumed that more abundant species will be more likely to have interactions (passive sampling), which then leads to nestedness (Araujo et al., 2010b; Vázquez et al., 2005). However, some research has called this into question (Corso et al., 2008; Rohde et al., 1998). Specifically, are generalists generalists because of their abundance, or *vice versa*, and does species abundance necessarily lead to the frequency with which that species interacts (Bascompte and Jordano, 2007; Santamaría and Rodríguez-Gironés, 2007; Stang et al., 2007)? Although the frequency with which individuals of a species are observed is likely to be related to their abundance, influencing their empirical “specificity”, this does not explain all of the nestedness observed in systems (Krishna et al., 2008; Nielsen and Bascompte, 2007), nor does it explain the presence of significantly anti-nested host-parasite networks (Joppa et al., 2010) and other patterns of nestedness (Hernandez and Sukhdeo, 2008; Lafferty et al., 2006). Indeed, a number of sources highlight the importance of a variety of simultaneous mechanism leading to nestedness (Bastolla et al., 2009; Fontaine et al., 2009; Rezende et al., 2007; Vázquez et al., 2009a). Krishna et al. (2008) even demonstrate that, although abundance and trait matching separately can be seen to influence nestedness, considering the two together provides a far better predictor.

Secondly, phenotypic complementarity refers to trait matching between species, for example in nectar holder size and length (Rezende et al., 2007; Vázquez et al., 2009a). An equivalent idea in antagonistic webs to phenotypic trait complementarity in mutualistic webs is the concept of barriers to exploitation, where it is only worthwhile for a species to target another which is not protecting itself (Santamaría and Rodríguez-Gironés, 2007). Both of these concepts appear to be important in explaining interaction patterns, leading to forbidden links and overlapping trait-values (Bascompte and Jordano, 2007; Santamaría and Rodríguez-Gironés, 2007). The asymmetry of interaction strengths refers to the tendency of ecological specialization to create these forbidden interactions, between species which are unable to connect (Jordano et al., 2006; Ulrich et al., 2009). This is similar to phenotypic complementarity in that it refers to a kind of “uncomplementarity,” and occurs due to the values of phenotypic traits.

One point of contention in terms of nestedness is the effect of sampling bias. Previously, this was used by Blüthgen et al. (2008) to explain nestedness, throwing the question of the occurrence of extensive patterns of nestedness into doubt. However, this calculation was conducted using the temperature metric, unlike more recent data (Graham et al., 2009; Joppa et al., 2010), which

corrects for matrix dimension and fill. Additionally, some sources (Baněšek-Richter et al., 2004; Gibson et al., 2011; Nielsen and Bascompte, 2007; Vázquez and Aizen, 2006) have shown that sampling effort has very little effect on nestedness, specifically when using the NODF metric rather than temperature (Rivera-Hutinel et al., 2012), and indeed Dorado et al. (2011) have shown that improved sampling should increase nestedness. Clearly this is a contentious issue, and one which we do not address here.

There appears to be a combination of evidence justifying the validity of each potential driving force of nestedness, and it seems unlikely that, even if one is dominant, the others would have no effect (Vázquez et al., 2005, 2009b). Indeed, Olesen et al. (2008) saw a link between nestedness and abundance as well as nestedness and phenophase length (which is a result of complementarity/forbidden links). Stang et al. (2007) found a strong link between specialization asymmetry and nectar-holder size (a phenotypic trait) followed by abundance. Although this does not necessarily result in a similar link to nestedness, as nestedness implies specialization asymmetry but not *vice versa* (Bascompte and Jordano, 2007; Jordano et al., 2006), it is a promising sign. Our approach here is compatible with the concept of abundance, and indeed demonstrates a mechanism by which the effects of relative species abundances might lead to nestedness (M^cQuaid and Britton, 2012), but we cannot here consider the effects of sampling. Suffice to say that we attend to the pattern of nestedness, relying on the above mentioned studies as a proof that patterns of nestedness are indeed significant in host-parasite networks, and are unlikely to occur due to sampling error or abundance alone.

We therefore propose a model host-parasite network driven by trait co-evolutionary trade-offs that includes a combination of influences from abundance, forbidden links and trait-matching, as it seems likely that evolutionary history and ecological factors together shape the structure of networks (Bascompte and Jordano, 2007; Blüthgen et al., 2007). Each species in our host-parasite system is assumed to have limited resources to use in interacting with all species from the opposite group (parasites or hosts respectively). These resources are focused on the transmission of infection, with parasites aiming to increase transmission while hosts attempt to decrease transmission. In M^cQuaid and Britton (2012), an exploratory model was proposed for a four-species system, with two hosts and two parasites. Here, this is expanded to a system with m hosts and n parasites, while remaining identical in its core principles. Results are then given for $m = n = 5$. The aim of this is to discover whether the simpler model seen in M^cQuaid and Britton (2012) can explain patterns of nestedness in a larger system.

This paper begins by outlining the model of M^cQuaid and Britton (2012), before describing some of the difficulties encountered in adapting it to a higher dimension. This is followed by a discussion of a series of evolutionary simulations and their resulting nestedness. Using the temperature and NODF metrics we found nestedness to occur more often than expected when trade-off shapes were weak (convex), while “anti-nestedness” occurred more often than expected when the majority of trade-off shapes were strong (concave).

2. The Model

This model uses a susceptible-infected system, with m host species and n microparasite species. S_i refers to susceptible hosts of species i , while I_{ij} refers to hosts of species i infected

by parasite species j , where in this instance $i \in \mathbb{N}_m$, $j \in \mathbb{N}_n$. We then have

$$\begin{aligned}\frac{dS_i}{dt} &= \alpha_i N_i - \sum_{j \in \mathbb{N}_n} a_{ij} c_{ij} S_i F_j^i - \omega_i S_i N_i, \\ \frac{dI_{ij}}{dt} &= a_{ij} c_{ij} S_i F_j^i - \gamma_{ij} I_{ij} - \omega_i I_{ij} N_i.\end{aligned}\tag{2.1}$$

The model birth (α_i) and death (ω_i) rates depend on the host species i , and there is an additional infection-related death term; death rate γ_{ij} of host species i due to parasite species j . $N_i = S_i + I_{i1} + I_{i2}$ represents the total population size of host species i .

The force of infection F_j^i of parasite species j on host species i is given by

$$F_j^i = \sum_{k \in \mathbb{N}_m} \beta_j^{ik} I_{kj},$$

where β_j^{ik} is the pairwise potential infectious contact rate for the transfer of parasite j from host k to host i . In our model, this is moderated by the strategies adopted by the parasite j and the host i involved. It is then effectively given by $G_j^i = a_{ij} c_{ij} F_j^i$, with $0 \leq a_{ij} \leq 1$, $0 \leq c_{ij} \leq 1$. Here a_{ij} is a parasite phenotypic trait defining the relative probability of success of parasite j 's attack on host i , and c_{ij} is a host phenotypic trait defining the relative probability of failure of host i 's defense against parasite j . Parasites benefit from high values of a_{ij} , while hosts benefit from low values of c_{ij} , reflecting the relative success or failure of transmission.

Species do not, however, have unlimited resources with which to ensure transmission or defense. Hence, our trade-off assumes that each parasite species j has a fixed amount of resource to allocate to infection of different host species i , where $i \in \mathbb{N}_m$. The trade-off is a negative, species-specific function, which is not dependent upon the population or environment. Similarly, a host species i varies strategy c_{ij} in order to reduce transmission of parasite j , where a similar trade-off is presumed. The transmission of infection to a susceptible host is now dependent on the force of infection and the relevant strategies which both host and parasite have adopted. As the trade-off shape can have an important effect on evolution (Best et al., 2009; Kisdi, 2006; Rueffler et al., 2006), we have assumed a trade-off shape here which can be altered to be either strong or weak, determined by a species-specific power (θ_j for parasite species j and ϕ_i for host species i). We have that

$$\sum_{i \in \mathbb{N}_m} a_{ij}^{\theta_j} = 1 \quad \text{and} \quad \sum_{j \in \mathbb{N}_n} c_{ij}^{\phi_i} = 1.\tag{2.2}$$

Note that $a_{ij} \in [0, 1]$ and $c_{ij} \in [0, 1]$ for all i, j . For parasite species j , $\theta_j < 1$ implies a strong trade-off, and $\theta_j > 1$ implies a weak trade-off. A parasite is a perfect generalist if $a_{ij} = (\frac{1}{m})^{\frac{1}{\theta_j}}$ for all i , which is henceforth termed the *neutral point*. At this point all trait-values for that parasite are equal, so it is investing equally in targeting all host species. Note, however, that different levels of defense by the host species may affect the relative success of the parasite in each species. The parasite is a complete specialist in host k if $a_{kj} = 1$ and $a_{ij} = 0$ for all $i \neq k$. In this case, it invests all of its resources in one host species only. Host species trade-off their resources in a similar manner. Because species cannot co-infect a host, any infected host is unavailable to other parasites of all species, reducing the susceptible class. Hence, parasite species compete to infect any shared host species. A detailed analysis of the model where $m = n = 2$ can be found in McQuaid and Britton (2012).

3. Method

We used the technique of adaptive dynamics to analyze the model, which assumes that rare mutations occur, producing mutants with marginally different phenotypic effects to residents. These mutants can only invade the population if their growth rate is positive in an equilibrium environment of residents. In that case, the population of mutants has the potential to grow in size over ecological time until the mutant phenotype becomes dominant and excludes residents (Dieckmann and Law, 1996; Geritz et al., 1998; Metz et al., 1996). Events are thus separated into evolutionary and ecological time-scales (Drossel and McKane, 2005). M^cQuaid and Britton (2012) give a full analysis for a smaller system. Here, though, mutations occur between two trait-values during any evolutionary time-step; as a species' trait value with respect to an opponent mutates up, the trait value with respect to one other opponent must be reduced at random, as a consequence of the equality in Eq. 2.2. Investigations using a full trade-off between all traits, as used by Dieckmann and Law (1996), were unable to satisfy this constraint. Therefore, evolution was partitioned into steps, and in each step a mutant of one random species with a slight variation in two random traits was introduced to the system (satisfying the invasion conditions given in M^cQuaid and Britton, 2012). A successful mutant then replaced the resident, and the next evolutionary step was calculated at the new equilibria containing the mutant. An example of the process of evolutionary change in trait values with time where $m = n = 3$ is given in Fig. 2. In this example, the final interaction matrix (of relative population densities) is given by M_1 , and can be rearranged to give M_2 , where

$$M_1 = \begin{pmatrix} 8 & 1 & 0 \\ 8 & 0 & 0 \\ 0 & 8 & 8 \end{pmatrix} \text{ and } M_2 = \begin{pmatrix} 0 & 8 & 8 \\ 8 & 1 & 0 \\ 8 & 0 & 0 \end{pmatrix}, \quad (3.3)$$

where columns represent parasites and rows hosts. Comparing this to Fig. 1(c), we see that this displays specialization asymmetry, but not nestedness.

To simulate this system, a range of trade-off types were investigated, and in each case a sample of matrices resulting from different initial trait-values were calculated. The initial trait-values of the system were important in calculating evolutionary change, producing a range of different results. Unfortunately, the space of all possible initial trait-values was very large. We therefore defined the initial host trait-values to display equal investment in each parasite species, and chose parasite initial trait-values using rejection sampling. A population size matrix was constructed using the resulting evolutionary trait-values after a set period of time, when a pattern emerges as the system reaches a noisy, but stable, end-point. This burn-off period was established using test simulations. Note that, potentially due to the lack of an imposed structure, which ensures that parasites or hosts could mutate trait values away from a potential threat, no species extinctions were ever witnessed. Whereas in M^cQuaid and Britton (2012) trait values were investigated for nestedness, here the size of a population infected with a particular parasite was used, with the number of infected hosts representing the population size. The resulting matrix was then tested for nestedness using the WNODF program of Almeida-Neto and Ulrich (2011) to measure nestedness according to the temperature index of Atmar and Patterson (1995, 1993), the discrepancy metric (Brualdi and Sanderson, 1999), the NODF metric (Almeida-Neto et al., 2008) and the weighted WNODF metric (Almeida-Neto and Ulrich, 2011).

When constructing null models, we chose to re-sample keeping row and column sums fixed, as this should lead to more type II errors and so our results would be less likely to incorrectly

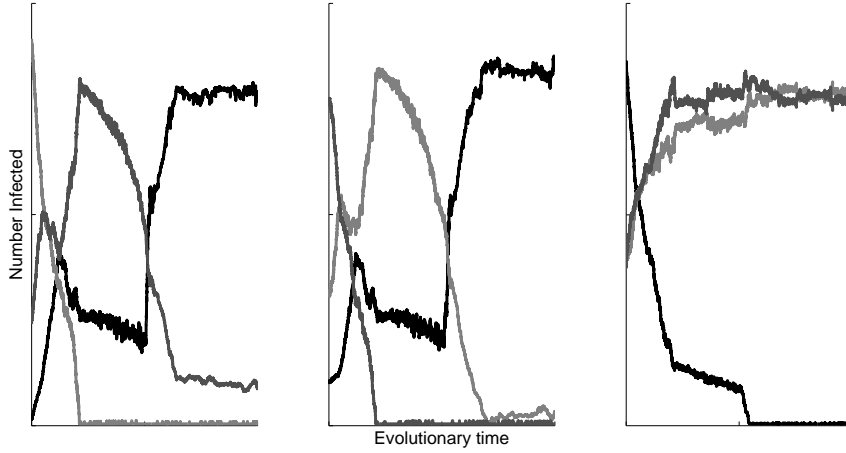


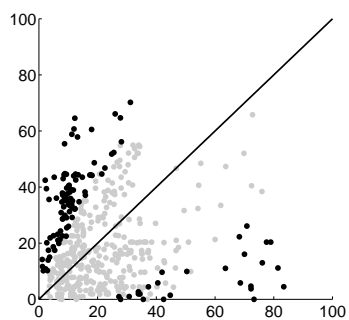
Figure 2: Example of the evolution of trait values in a system with 3 hosts and 3 parasites. Each line follows the evolution of the combined trait values of a specific host and parasite, to give the relative level of infection. Plots represent different hosts, and line shades different parasites. For example, the first plot represents the infection levels of all 3 parasites in the first host. The darkest (black) lines follow the infection levels of one particular parasite across all 3 hosts. The final infection levels, after a burn-off period, are used to create a matrix of species interactions, from which the nestedness is calculated.

find nestedness. We used a larger number of matrices than the default for computing confidence limits, as this was suggested for smaller matrices (Almeida-Neto and Ulrich, 2011). The matrices were packed according to species and weight.

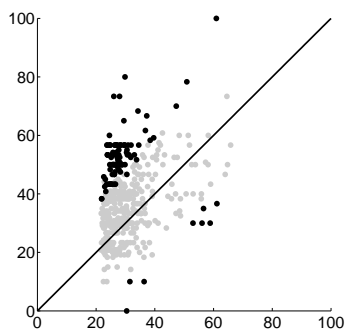
Tests for nestedness yielded Z-scores obtained according to the following metrics: discrepancy, temperature, NODF and WNODF. Results included the Z-score and whether or not that Z-score was significant for each network at the 5% level. In order to discover whether our results demonstrated nestedness, we tested them as follows. Firstly, due to the random null models we compared the data to, in order to detect nestedness, we would expect 5% of matrices to be both unusually nested and unusually anti-nested (or hot, depending on the metric) (Joppa et al., 2010). In order to discover if more networks than expected fell into the range of unusually nested or anti-nested, we used a Chi-square test to compare the expected values. If we discovered that a significant number of networks were unusual, then we used a binomial test to discover whether there was a significant difference between the number of matrices that were unusually nested and those that were unusually anti-nested. This was repeated for a range of trade-off shapes, including weak trade-offs only, strong trade-offs only, a mixture with two weak and three strong trade-offs and *vice versa*.

4. Results

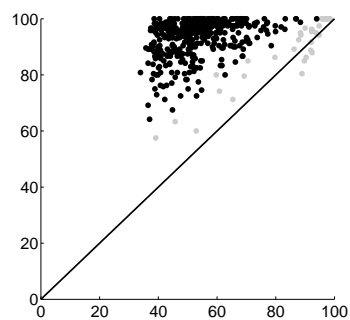
Our results are all given here at the 5% level of significance. In Fig. 3 we see for a range of trade-off strengths and metrics whether the resulting matrices were significantly different from null models. Here, black dots represent matrices that were significantly different, while gray dots represent those that were not. The line indicates the diagonal, where the observed and expected



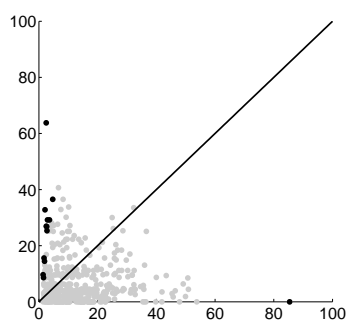
(a)



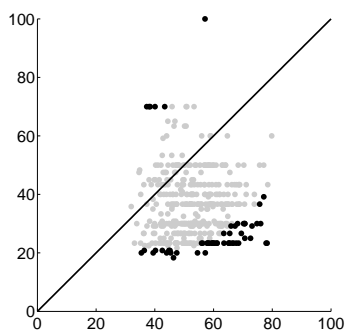
(b)



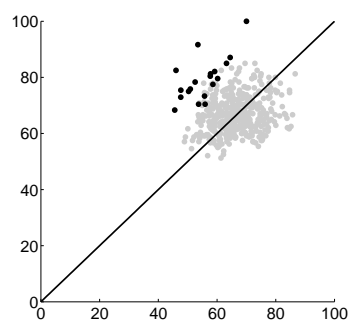
(c)



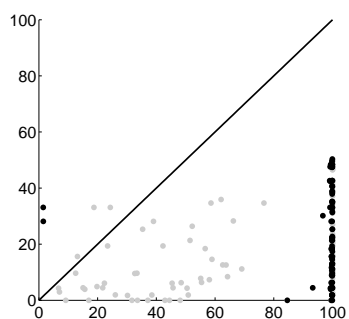
(d)



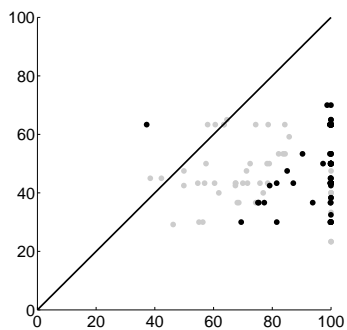
(e)



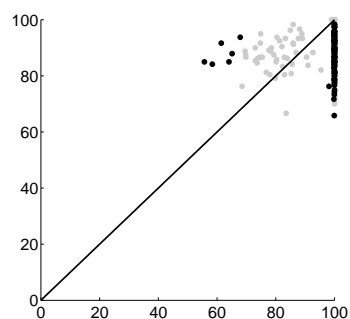
(f)



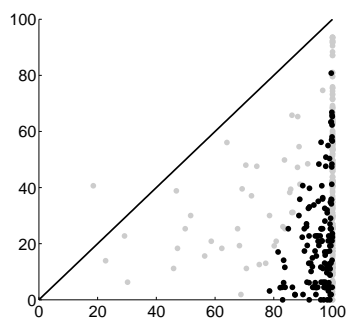
(g)



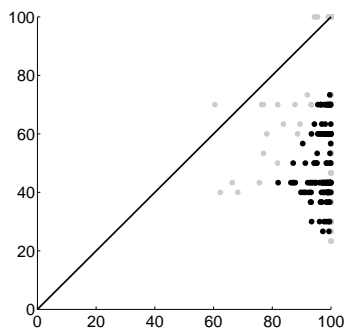
(h)



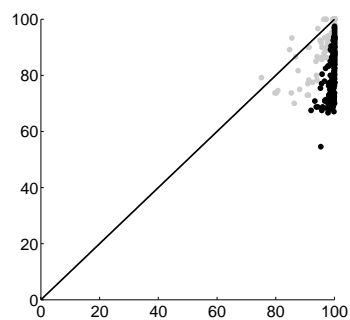
(i)



(j)



(k)



(l)

Figure 3 (previous page): A comparison of three of the metrics used to test for nestedness in systems with different strengths of trade-off in resources for parasite species. The x-axes here are the mean measurements (according to each specific metric) for 10 000 null models. The y-axes are the measurements taken from the observed matrices. Each column of sub-figures considers a different metric; plots (a, d, g, j) use the temperature metric (Atmar and Patterson, 1993), plots (b, e, h, k) use the NODF metric (Almeida-Neto et al., 2008) and plots (c, f, i, l) use the WNODF metric (Almeida-Neto and Ulrich, 2011). Each row of plots represents trade-offs of a different strength. Trade-off strengths are strong for all parasite species in plots (a–c), strong for a predominant proportion of parasite species in plots (d–f), weak for a predominant proportion of parasite species in plots (g–i) and weak for all parasite species in plots (j–l). We have re-scaled the metrics NODF and WNODF so that they may be compared to the temperature metric. Hence, for all three metrics, a value of 0 indicates perfect nestedness, while a value of 100 indicates “anti-nestedness.” Black dots represent those matrices for which the Z-score ($\frac{Obs-Exp}{StDevExp}$) is significantly different from zero at a 5% level of confidence (Almeida-Neto and Ulrich, 2011). Grey dots represent those matrices for which the Z-score is not significantly different from zero. The solid line is the line $x = y$, and hence any points below the line are more nested than expected, while those above are less nested than expected.

values for matrices were equal. Any matrices to the right of the diagonal, therefore, were more nested than expected, while any to the left were less nested.

We see in table 1 that in almost every case with every metric there was an unusually high number of non-random networks. The temperature, NODF and WNODF metrics were generally in agreement, with a low temperature occurring at the same time as significantly nested structures, and a high temperature occurring simultaneously to anti-nestedness. Interestingly, the discrepancy metric showed that not a single combination of trade-off strengths resulted in nestedness. There was always an unusual high number of matrices which had significantly high discrepancies, indicating a lack of nestedness (Brualdi and Sanderson, 1999). This could be due to the null model used, which increases the chances of incorrectly failing to reject the null hypothesis of no nestedness.

Ignoring the discrepancy metric, we see that if all parasite species have a strong trade-off, then each metric finds an unusual number of significantly anti-nested or hot networks. If all parasite species have weak trade-offs, or in fact if three out of five of parasites have weak trade-offs, then all three metrics (ignoring the discrepancy metric) find an unusually high number of significantly nested networks. If only two out of five of parasites have a weak trade-off, and the other three strong, however, then the results are more complicated. Here, both temperature and WNODF found that there were unusually fewer significantly nested or anti-nested networks than expected by chance. The results were random, with both less nestedness and anti-nestedness than expected by chance. The NODF metric, on the other hand, still found an unusual number of significantly nested networks.

5. Discussion

These results seem to be indicative of a fairly strong trend. Firstly, most forms of trade-off seem to yield a very strong structure. If trade-offs are weaker, then this is highly likely to be nested, whereas the more strong trade-offs there are the more likely the system is to exhibit anti-nestedness. This is in reasonable agreement with Joppa et al. (2010) and Poulin and Guégan (2000), who found, in host-parasite and -parasitoid webs, that there were an unusually high

Metric	Trade-off							
	Strong		Mixed strong		Mixed weak		Weak	
	sig	sign	sig	sign	sig	sign	sig	sign
Disc	✓	—	✓	—	✓	—	✓	—
Temp	✓	—	✗	0	✓	+	✓	+
NODF	✓	—	✓	+	✓	+	✓	+
WNODF	✓	—	✗	0	✓	+	✓	+

Table 1: Table of results for different trade-off strengths under different metrics. Metrics include discrepancy (Brualdi and Sanderson, 1999), temperature (Atmar and Patterson, 1993), NODF (Almeida-Neto et al., 2008) and WNODF (Almeida-Neto and Ulrich, 2011). Trade-off strengths are either strong for all parasites, a mixture which is predominantly strong or predominantly weak, or weak for all parasites. One column (sig) indicates whether or not the data contained an unusually high number of non-random networks according to each metric (at a 95% level of confidence), and a second (sign) whether any unusual results were significantly positive or negative. Note the discrepancy and temperature metrics are rescaled such that, in agreement with the NODF and WNODF metrics, a positive Z-score indicates nestedness.

number of non-random networks, which contained both significantly nested and significantly anti-nested webs. In addition to this, Joppa et al. (2010) even suggested that the anti-nestedness might be due to co-evolution, as our data suggest. It seems, then, that our proposed model could indeed correctly drive patterns of nestedness and anti-nestedness in host-parasite food webs, a concept which is corroborated by a number of different metrics.

The agreement of these results over a range of metrics is promising, supporting our conclusions. The failure of the discrepancy metric to agree with all except one of our results suggests that it may be an inappropriate metric to use, possibly due to the size of the networks, where nestedness is much less likely to be evident in both real-world and model networks (Guimarães Jr and Guimarães, 2006; Joppa et al., 2010; Santamaría and Rodríguez-Gironés, 2007). In small networks, the influence on nestedness of different species with an identical number of interactions is felt, promoting the possible incorrect acceptance of a null hypothesis of no nestedness (Almeida-Neto and Ulrich, 2011; Araujo et al., 2010a; Podani and Schmera, 2012). The remaining metrics appear less affected by this, and seem fairly interchangeable. The most reliable metric is likely to be the weighted WNODF metric, which considers interaction strengths, through population size, rather than binary data. It is, however, comforting that this metric agrees with both the temperature and NODF metrics, which have been used in the majority of empirical studies.

One important aspect to consider is the meaning of the term anti-nestedness. Here we simply use this to describe the results obtained according to the metrics used, but the actual physical representation of anti-nestedness may take on different forms depending on the metric and its authors' definitions. Almeida-Neto et al. (2007) describe the manner in which, for example, the term anti-nestedness has been used to describe random networks (Wright et al., 1998), checkerboard patterns (Duponte et al., 2003) and species absence from richer sites (Poulin and Guégan, 2000), amongst others. Here, to save confusion, we simply refer to anti-nestedness according to the metric.

Unlike M^cQuaid and Britton (2012), where specialization asymmetry was more evident in a system with strong or mixed trade-offs, our results show that in a larger system it is the presence of weak trade-offs that promotes nestedness. A caveat to this, however, is that even here we still

analyzed only a very small network. This should lead to lower than expected levels of nestedness (Guimarães Jr and Guimarães, 2006), and could significantly affect results. Unfortunately, due to computational times and the variety of possible initial trait-values (which have a significant effect on results, see McQuaid and Britton, 2012), investigating larger networks was not feasible. In addition to this, altering the mutation rates of hosts compared to parasites (as in McQuaid and Britton, 2012) might also suggest useful avenues for experimental research, predicting the circumstances under which we would expect to see nestedness. Again, however, computational constraints severely limit this.

We propose here that the manner in which species make the best use of their limited resources leads to patterns of nestedness in host-parasite webs. This is influenced by both abundance and phenotypic trait-matching. Indeed, as this involves the evolution of trait values, matching may in fact arise as a consequence of these trade-offs (see, for example, Blüthgen et al., 2007). Vital to this is the aspect of co-evolution, without which there could be no dynamical matching of traits. Although host evolution has often been ignored in the past, due to longer generation times and smaller populations, it is becoming clear that even low rates of evolution for hosts can have an effect on evolutionary outcomes Best et al. (2009). Our paper demonstrates that the co-evolution of multiple species might, in fact, be key to understanding the structure and function of inter-species relationships. Unfortunately, it also highlights the importance that chance can have in such large systems. For example, in Fig. 3(a) it appears that a system can evolve to be either significantly nested or significantly anti-nested depending on the initial trait-values (in relation to evolutionary repellers) and the stochastic evolutionary process, demonstrating that suitable repetition and care is required when investigating the co-evolution of large networks.

The quantification and understanding of nestedness stretches beyond just one simple measure, as many network properties and patterns are inter-related (Burgos et al., 2007; Fortuna et al., 2010). Hence, the use of a dynamical model explaining one such pattern leaves many open questions concerning others, and any predictions that the model makes regarding them. There is a scarcity in research of dynamical models containing many species, and these could in fact be key to explaining nested trophic links (Montoya et al., 2006). This nested structure, of a core of species responsible for the majority of interactions, and an asymmetry in interactions, may be vital for the robustness of food webs (Jordano et al., 2006). Having demonstrated the application of trade-offs to host-parasite webs, it would be beneficial to repeat this for mutualistic webs, which have much higher levels of nestedness and no anti-nestedness (Joppa et al., 2010). For a host-parasite system, however, our trade-off concept can be used to explain nestedness, predicting a significant number of nested networks if most parasite trait trade-offs are weak, while predicting a higher number than expected of anti-nested networks if most trade-offs are strong.

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